AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 103:163–171 (1997)

Affiliative Relationships Between Adult Males and Immature Group Members in Naturally Occurring Ringtailed Lemurs (*Lemur catta*)

LISA GOULD*
Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 2H4, Canada

KEY WORDS affiliative behavior; ringtailed lemurs; adult males; immatures

ABSTRACT Affiliative relations between adult males and immature group members were studied in three naturally occurring groups of ringtailed lemurs (*Lemur catta*) over a 12-month period at Beza-Mahafaly Reserve, southwestern Madagascar. No statistically significant difference was found in rates of affiliative interactions between adult males and older immatures (juveniles and adolescents) over reproductive seasons. However, some of the adult males in two focal groups increased their rates of affiliative behaviors with older immatures during the lactation and subsequent 1993 postmigration periods. Female involvement with infants during lactation season, the increasing independence of juveniles and adolescents, and length of male tenure may be factors contributing to such a pattern. Neither adult males nor immatures were significantly responsible for the initiation and maintenance of proximity in male-immature dyadic interactions. Neither dominance rank nor age-class of the adult male affected their rates of affiliative behavior with immatures. The majority of focal males exhibited an interest in infants and occasionally participated in alloparental care. It is suggested that adult males can benefit from affiliative relations with immatures in terms of opportunities for greater spatial centrality in the group, which can lead to enhanced predator protection and greater opportunities to develop affiliative relationships with females. Immatures can benefit from affiliation with males in relation to enhanced predator detection and protection, alloparental care, and opportunities to develop social skills. Am J Phys Anthropol 103:163–171, 1997.

Among anthropoid primates living in multimale-multifemale social groups and characterized by male dispersal, affiliative behavior between adult males and immature group members varies considerably. It ranges from intensive in Barbary macaques (Taub, 1984) to moderate or relatively infrequent and seasonal in Japanese macaques, rhesus macaques, and savannah baboons (Itani, 1959; Alexander, 1970; Hasegawa and Hiraiwa, 1980; Packer, 1980; Hill, 1986; Altmann, 1980; Strum, 1984; Smuts, 1985).

Several variables have been suggested to affect male-immature affiliative relationships and alloparenting. For example, in a number of macaque species and in vervet monkeys, younger adult males interact more with immatures than older males (Alex-

Contract grant sponsor: National Science Foundation Grant; contract grant number BNS-91191122; contract grant sponsor: Wenner-Gren Pre-doctoral Research Grant; contract grant number 5401; contract grant sponsor: National Geographic Research Grant; contract grant number 4734-92; contract grant sponsor: Boise Fund of Oxford; contract grant sponsor: Alberta Heritage Scholarship.

*Correspondence to: Lisa Gould, Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 2H4, Canada. E-mail: lisa.gould@ualberta.ca

Received 16 July 1996; revised 12 March 1997; accepted 16 March 1997.

ander, 1970; Breuggerman, 1973; Taub, 1984; Fairbanks, 1993). High-ranking rhesus macaque males affiliate more with immatures than lower-ranking males (Breuggerman, 1973; Hill, 1986). Finally, males with longer tenure in a group interact with infants and exhibit caretaking behaviors more frequently than recent immigrants in baboons, rhesus macaques, and vervets (Packer, 1980; Vessey and Meikle, 1984; Horrocks and Hunte, 1993).

Reproductive seasonality can also affect social relationships between adult males and immatures. In Japanese and rhesus macaques, Itani (1959), Alexander (1970), Hasegawa and Hiraiwa (1980), Gouzoules (1984), and Hill (1986) found that alloparenting and affiliative behavior between males and older immatures (1- and 2-year-olds) were either more frequent or occurred exclusively during the birth season when mothers were involved with care of newborns.

Immatures benefit from affiliative associations with adult males in terms of protection from predators or other group members in baboons (Ransom and Ransom, 1971; Altmann, 1980; Packer, 1980; Smuts, 1985) and Japanese and Barbary macaques (Itani, 1959; Taub, 1984). Immatures have greater access to food resources in rhesus macaques and vervets (Hill, 1986; Horrocks and Hunte, 1993). Adult males may also benefit from affiliative contact with immatures in a variety of ways. Suggested benefits include integration into a social group in rhesus macaques (Hill, 1986) and self-protection by using infants as "buffers" in agonistic interactions with other males in Barbary and bonnet macaques and baboons (Deag and Crook, 1971; Taub, 1980, 1984; Silk and Samuels, 1984; Kummer, 1967; Busse and Hamilton, 1981; Strum, 1984; Hamilton, 1984; Smuts, 1985). Other benefits may be maintaining paternal investment in baboons and rhesus macaques (Smuts, 1985; Hill, 1986) or enhancing mating success by establishing an affiliative relationship with an infant's mother in baboons and in Japanese and Barbary macaques (Altmann, 1980; Takahata, 1982; Taub, 1984; Strum, 1984; Smuts, 1985).

All of the above mentioned examples occur in species in which males are dominant to females. Patterns of adult male–immature affiliation, and benefits accruing from such relationships, may differ in a species such as the ringtailed lemur (*Lemur catta*) in which females are dominant to males in all feeding and social contexts (Jolly, 1966; Taylor and Sussman, 1987; Pereira et al., 1990). For example, immatures may not benefit from proximity to adult males through greater access to food resources, or protection from other group members in a female-dominant primate, as females have priority of access to all resources and are the primary defenders of the home range. Thus, the adaptive value of adult male–immature affiliative relationships may differ from that proposed for male-dominant primates.

This paper will focus on the affiliative relationships between adult males and immatures (2 years of age and under) in ringtailed lemurs and consider the potential benefits of such relationships to males and immatures, specifically whether rates of affiliative interactions between adult males and immatures vary according to reproductive season; whether immatures approach and maintain proximity with adult males more than vice-versa; and whether the dominance rank or age of the male or the length of tenure of an adult male in his group affects his rates of affiliative behavior with the immatures in the group.

METHODS

Study site and focal animals

This study of adult male–immature social relationships was part of a larger study of affiliative behavior patterns between adult males and all age-sex classes of conspecifics (Gould, 1994, 1996, 1997). The research took place between March 1992 and March 1993 at Beza-Mahafaly Special Reserve, 23°30′S lat., 44°E long., in southwestern Madagascar, 35 km east of the town of Betioky-Sud (Sussman, 1991). Ringtailed lemurs occur only in south and southwestern Madagascar, and primarily occupy riverine and xerophytic forests (Jolly, 1966; Sussman, 1977). Group size ranges from approximately five to 27 individuals, with adult sex ratios of 1:1 (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1977). This species exhibits strict reproductive seasonality in both the female reproductive cycle and male migration (Jolly,

1966; Sussman, 1977, 1992; Jones, 1983; Sauther, 1991).

Nine social groups of ringtailed lemurs live within the Beza-Mahafaly Reserve boundaries; of these, three were chosen for study. Age-class and migration status were known for all focal males in the study, as animals in all groups living in the reserve are part of a long-term demographic project on ringtailed lemurs begun in 1987, and are tagged and collared for identification purposes (Sussman, 1991).

It was not possible to identify individually the immatures in the groups, as animals under 2 years of age are not captured and given identification collars and tags. Thus, when immatures are high in the canopy they are not distinguishable from each other. However, the age-classes of the immatures were known, because ringtailed lemurs are seasonal breeders, and infants are born within a 3-week period once a year. This is reflected through marked differences between the body sizes of infants (0–6 months during the study period), juveniles (6–18 months), and adolescents (18–30 months).

Data collection and analysis

Over a 12-month period, 1,102 hours of focal animal data on the affiliative behavior of nine adult males in three social groups were collected. The order of focal animal sampling was equally rotated and determined at the onset of each week of data collection. Data were collected during the focal groups' active periods, which varied according to season and temperature.

On-the-minute focal animal point sampling (Altmann, 1974) in the form of 1-hour sessions was the primary method of data collection. In addition, all occurrences (Altmann, 1974; Slater, 1978) of agonistic behaviors were recorded. Every 15 minutes, nearest neighbor data were collected. Such data included the individual identity (in the case of adults) or age-class (in the case of immatures) of all animals in contact, within 1 m, and within 3 m of the focal animal. During each 1-hour focal session, the activity in which the focal animal was engaged (taken from a detailed ethogram of ringtailed lemur behavior adapted from Jolly, 1966; Taylor, 1986; and Gould, 1989) was recorded at 1-minute intervals. If the behavior was affiliative in nature, the initiator and direction of the behavior were also recorded. To determine the actual frequency of affiliative behaviors, the onset of a "bout" of an affiliative interaction between a focal animal and another group member was coded differently from the same behavior if it occurred for a duration of more than 1 minute. For example, if a focal animal was engaged in a mutual grooming session with a partner for 5 minutes, the first 1-minute interval was recorded as "onset of mutual grooming with partner X," and the remaining four intervals were recorded as "mutual grooming with partner X." Thus, when the data were analyzed, it was possible to obtain frequencies of the affiliative interactions of the focal males by tallying the number of "onsets."

To obtain rates per hour of affiliative interactions across reproductive seasons, the frequency of each focal male's affiliative interactions was divided by the number of hours of data collected on that animal in the particular season in question.

Behaviors considered affiliative

Affiliative behavior between adult males and immatures included sitting or resting in close proximity to ($<$0.5 m) or in contact with immature group members (any type of body contact), mutual grooming, one-way grooming, and huddling (when groups of two or more animals rest in full-body contact with tails wrapped around each other). In the case of male relations with infants, mutual grooming, resting, sitting, or feeding near ($<$0.5 m), or sitting or resting in contact with infants was considered affiliative behavior, and grooming and carrying of infants was considered alloparental care.

Group composition

Group composition was as follows: Blue group, 2 adult males, 3 adult females, 1 adolescent male; Green group, 2 adult males prior to migration season, 4 adult males after migration season, 5 adult females, 2 juveniles (sexes unknown), 2 adolescent males, 2 adolescent females; Red group, 5 adult males before migration season, 3 after migration season, 4 adult females, 3 juveniles (sexes unknown).

TABLE 1. Approaches and maintenance of proximity between adult males and immatures according to focal group

Focal male	Immature age-class	%ap(A) − %Lv(A)[1]	Responsible for maintaining proximity
Blue group			
B1	Adolescent male	52.9 − 47 = 5.9	B1
B2	Adolescent male	62.5 − 12.5 = 50	B2
Green group			
G1	Juveniles	14.2 − 57.1 = 42.9	Juveniles
G1	Adolescent males	15.7 − 31.5 = −15.8	Adolescent males
G1	Adolescent females	13.3 − 13.3 = 0	Neither
G2	Juveniles	25 − 12.5 = 12.5	G2
G2	Adolescent males	53.3 − 40 = 13.3	G2
G2	Adolescent females	26.9 − 30.7 = −3.8	Adolescent females
G3, G4[2]			
Red group			
R1	Juveniles	40 − 24 = 16	R1
R2	Juveniles	30.7 − 38.4 = −7.7	Juveniles
R2	Juveniles	20 − 15 = 5	R2
Immigrant males before migration			
R3	Juveniles	27.2 − 27.2 = 0	Neither
R4	Juveniles	0 − 20 = −20	Juveniles

[1] Hinde's index: the percentage of all *approaches* between two animals A and B that were due to A (%Ap) minus the percentage of all *leaves* due to A (%Lv). If the resulting value is positive, animal A is primarily responsible for maintaining proximity in the dyad. If negative, animal B is responsible for maintaining proximity.
[2] Insufficient data on the two immigrant males during and after immigration to calculate Hinde's index.

Dates of reproductive seasons

Designated dates for reproductive seasons were as follows: postmigration 1992, 14 March 92–13 May 92; mating, 14 May 92–12 June 92; gestation, 13 June 92–24 September 92; lactation and migration (concurrent), 25 September 92–25 January 93; postmigration, 1993, 26 January 93–13 March 93.

Determination of proximity maintenance

To determine if there were trends in proximity maintenance between adult males and immatures in affiliative relations, the index described by Hinde (1977) was used: %Ap(A) − %Lv(A). This calculation is done by taking the percentage of all *approaches* between two animals A and B that were due to A (%Ap) minus the percentage of all *leaves* due to A (%Lv). If the resulting value is positive, this indicates that animal A is primarily responsible for maintaining proximity in the dyad. If the value is negative, then animal B is chiefly responsible for maintaining proximity (Table 1).

RESULTS

Affiliative behavior across reproductive seasons between adult males and older immatures (juveniles and adolescents)

Friedman's two-way analysis of variance detected no significant differences in the rates of affiliative behaviors between adult males and older immatures and reproductive season. However, some trends existed. Males in two of the three study groups (Blue and Red groups) exhibited an increase in their rates of affiliative behavior with the older immatures in their groups (juveniles and adolescents) during the lactation and postmigration periods (25 September 1992 to 13 March 1993, Fig. 1). In all cases, these males had immigrated into their respective groups a few months prior to the onset of the study in 1992, and by postmigration season 1993 had resided in their groups for over 1 year, and were integrated members of the groups.

Proximity maintenance between males and immatures

In 46% of all male-immature dyads, the adults were responsible for maintaining proximity, and in 39% the immatures were responsible. In 15% of the cases, neither was responsible.

Dominance rank and affiliation with older immatures

The Mann-Whitney U-test showed no significant difference between higher- and lower-ranking males and their rates of affiliative behavior with older immatures (juve-

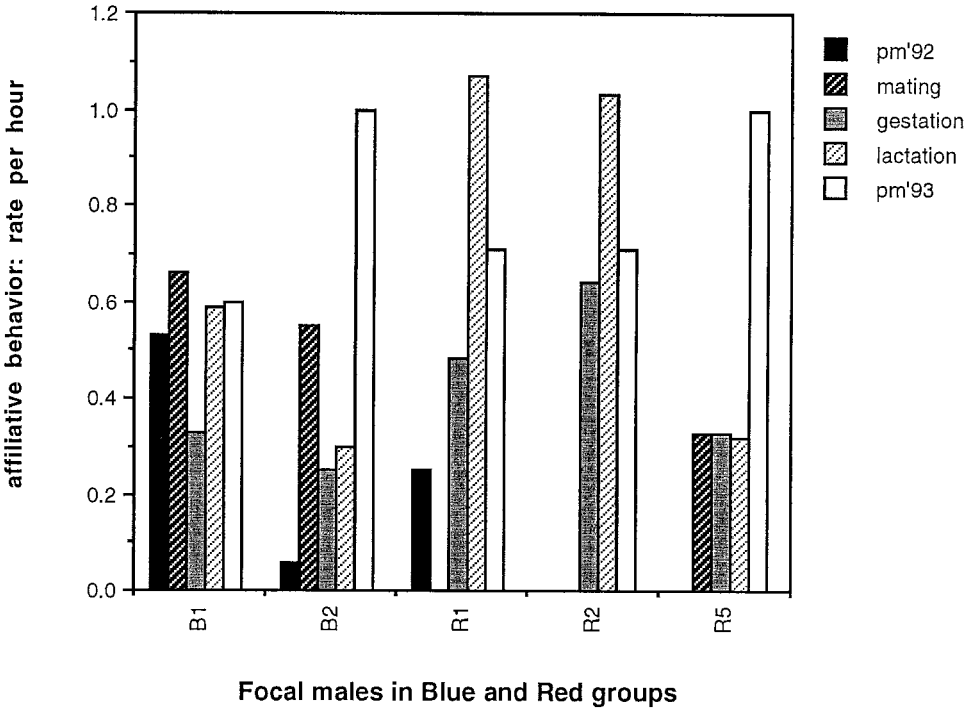

Fig. 1. Rates of affiliative behaviors between the adult males and the immatures in the Blue and Red groups over the five reproductive seasons during the 12-month study period: pm'92, postmigration period 1992 (14 March–13 May); mating, mating season 1992 (14 May–12 June); gestation, gestation period 1992 (13 June–24 September); lactation, birth and lactation period, concurrent with migration season (25 September 1992–25 January 1993) 1992–93; pm'93, postmigration period 1993 (26 January–13 March).

niles and adolescents). There were numerous changes in the male dominance hierarchy in all three focal groups during the year-long study, particularly during the first 6 months; thus, Figure 2a presents male affiliation with older immatures during the latter half of the study, when male dominance rank was more stable.

Affiliative behavior between adult males and infants

Three infants were born into each of the three study groups between 25 September and 5 November 1992. All nine infants disappeared between the ages of 2 weeks and 16 weeks. Infants disappeared at night, and primarily during the period of development when they were becoming independent from the mother with respect to locomotion and feeding. The birth and early lactation season of 1992 occurred at the end of a period of serious drought in the region, and both infant and adult female mortality were extremely high (Gould et al., 1996).

Blue group infants disappeared at 3, 10, and 15 weeks, Green group infants at 2, 5, and 14 weeks, and Red group infants at 10, 11, and 16 weeks. Thus, in each group, adult males had a minimum of 3 months available to interact with infants in their groups.

Six of the nine focal males were observed participating in alloparental or affiliative behavior with infants. Again, the Mann-Whitney U-test found no rank-related differences. Figure 2b presents the rates per hour of affiliative and/or alloparental behavior between the focal males and infants.

Age of adult males and affiliative relations with immatures

When younger (<5 years) and older adult males (>5 years) were compared, there was

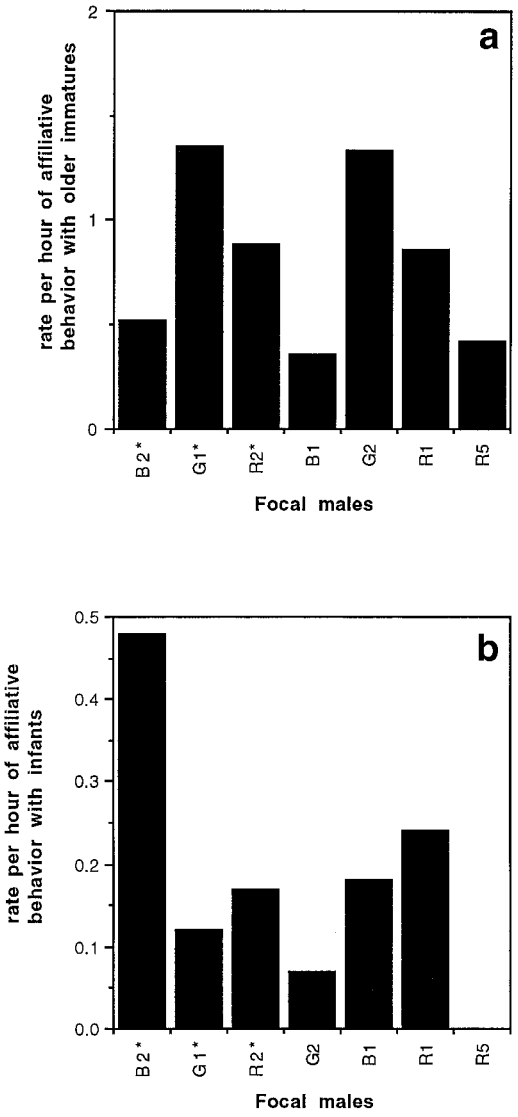

Fig. 2. **a:** Rank of the focal males and rates of affiliation with older (1- and 2-year-old) immatures. Asterisks indicate the highest-ranking males in their respective groups (Blue, Green, and Red groups). The two males that transferred from the Red to the Green group are not included in this analysis, as they were in the process of migration during the lactation season, and did not interact with older immatures in either group during this time. **b:** Rank of the focal males and rates of affiliation with the infants in their groups. Again, the three males with asterisks beside their names were the highest-ranking males in their respective groups.

no significant difference in their rates of affiliative behavior with immatures [Mann-Whitney U-test for very small samples (Siegal, 1956) N1 = 2, N2 = 7, $P > 0.05$].

DISCUSSION

In this study, significant seasonal differences were not found in relation to rates of male-immature affiliative interactions. Neither age nor dominance rank of the adult males affected their relationships with immatures, but length of residence in a social group did positively affect rates of affiliation between adult males and young animals.

Reproductive seasonality

Some of the focal males in two study groups (Blue and Red) exhibited higher rates of affiliative behaviors with the older immatures (juveniles and adolescents) during the lactation and subsequent postmigration periods. Female involvement in infant care during this period and the increasing independence of juveniles may be factors contributing to this result. Such a pattern has also been found in Japanese and rhesus macaques, wherein adult males affiliate with and care for yearlings and 2-year-olds almost exclusively during the birth season, when mothers are engaged in the care of newborns and have less time for their older offspring (Itani, 1959; Alexander, 1970; Hasegawa and Hiraiwa, 1980; Gouzoules, 1984; Hill, 1986).

Tenure and age effects

The focal males in Red and Blue groups that did exhibit increases in affiliation with immatures in the latter part of the study (lactation, postmigration, 1993) had just immigrated into their respective groups a few months prior to the onset of the study in 1992 (Sussman, unpublished data), and thus were unfamiliar with the immatures in their groups at the onset of the study period. Some of these males were spatially peripheral for several months after successful immigration. By the end of the study period, 1 year later, these males were well integrated. Therefore, length of tenure in a social group appears to have positively affected affiliative behavior with immatures in this case. Such a trend has also been found in adult male baboons, rhesus macaques, and vervet monkeys (Packer, 1980; Vessey and Meikle, 1984; Horrocks and Hunte, 1993).

Young adult male Japanese, rhesus, and Barbary macaques and young adult male

vervets have been found to affiliate more frequently with immatures than older males (Alexander, 1970; Breuggerman, 1973; Taub, 1984; Fairbanks, 1993). Among the ringtailed lemur males in this study, age did not have an effect on their frequency of affiliation with the immatures in their groups.

Proximity maintenance

Neither adult males nor immatures were significantly more responsible for proximity maintenance. This result contrasts with reports of male-immature proximity maintenance in some male-dominant primate species, where the immatures are much more responsible for maintaining the relationship than the adult males (Vessey and Meikle, 1984; Hill, 1986). Why was such a trend not found in ringtailed lemurs? It is suggested that adult male ringtailed lemurs do not provide certain benefits to immatures that males in some male-dominant species do. For example, they do not provide either protection from agonism by other group members or enhanced access to food resources, such as that reported for Japanese and Barbary macaques and savannah baboons (Itani, 1959; Ransom and Ransom, 1971; Altmann, 1980; Packer, 1980; Taub, 1984; Smuts, 1985; Hill, 1986; Horrocks and Hunte, 1993). This may explain why immatures do not seek out males as readily as immatures in some male-dominant species.

Dominance rank of the male

The dominance rank of the male ringtailed lemurs in the study had no effect on their rates of affiliative behavior with immatures. Much variation has been reported in relation to male dominance rank and interaction with immatures in some anthropoid species. For example, in rhesus macaques, both Breuggerman (1973) and Hill (1986) noted that the most persistent male/immature affiliative relationships involved the higher-ranking, most central males. Conversely, Estrada and Sandoval (1977) found that among adult male stumptail macaques, rank of the male was inversely correlated with the amount of infant care displayed. Taub (1984) reported that among Barbary macaques, the rank of the male was not a critical factor in the amount of infant caregiving an adult male performed. The ringtailed lemur males in the study groups appear to exhibit similarities to Barbary macaques with respect to dominance rank and affiliative interactions with immatures.

Adult male ringtailed lemurs do exhibit an interest in infants, and alloparental care and affiliative behavior between males and infant ringtailed lemurs at both Berenty Reserve (Gould, 1992) and Beza-Mahafaly Reserve (Gould, 1994) has been observed. It has been suggested that first mating in ringtailed lemurs may confer a paternity advantage (Pereira and Weiss, 1991; Sauther, 1991). However, in both the Blue and Red groups, the males that exhibited the highest rates of interactions with infants (B2 and R1) were not the first to mate with a number of the females (Gould, 1994). If first mating does correlate with paternity, paternity may not necessarily correlate with higher amounts of infant care.

Benefits to adult males and immatures of male-immature affiliative relationships

An affiliative relationship between an adult male and an immature group member can potentially benefit both animals in a number of ways. For an adult male, affiliation with infants and older immatures places a male in a more central position with respect to the female core of the group, since immatures stay in relatively close proximity to their mothers. Greater centrality can result in enhanced predator protection. Furthermore, greater centrality can result in better tolerance by females of a male's presence and, thus, potentially greater opportunities for a male to develop social relationships with females. Affiliative relationships with females are not only beneficial in a social sense, but also with respect to health and survival in the cold season. During the austral winter in southern Madagascar, temperatures can drop to as low as 3°C during the night, and reach only 18 or 20°C during the day. Morland (1993) suggests that animals that form large huddles during the cold season can benefit from enhanced thermoregulation, but that huddling requires a high degree of tolerance between animals. In ringtailed lemur groups, the largest huddles are made up of females, immatures,

and occasionally adult males. Forming affiliative relationships with immatures may result in acceptance into a huddle during the winter months. Males may also derive contact comfort from infants, as has been suggested by Strum (1984) for adult male olive baboons.

Immature ringtailed lemurs benefit from affiliative behavior with males with respect to predation detection and protection, alloparental care, and the opportunity to develop social skills which, particularly for male immatures, can be of great importance in terms of learning appropriate sex-specific behaviors.

Not all group-living lemur species are female dominant (Pereira et al., 1990). Future research on adult male relationships with immatures in other naturally occurring prosimian species exhibiting differing types of social organization and dominance patterns needs to be conducted. Such information can help us to gain a greater perspective on the variation in and adaptive significance of male-immature interactions in prosimian primates, as well as providing us with greater insight into this question as applied to the entire primate order.

ACKNOWLEDGMENTS

I thank Dr. R.W. Sussman for his advice and encouragement throughout this project. I also thank Drs. D.T. Rasmussen, J. Phillips-Conroy, F. Marshall, J. Losos, A. Templeton, and Z. Tang-Martinez and three anonymous reviewers for their helpful suggestions on various drafts of this manuscript. I am grateful to Mme. Berthe Rakotosamimanana, M. Pothin Rakotomanga, Dr. Andrianansolo Ranaivoson, M. Benjamin Andriamihaja, Mme. Celestine Ravaoarinoromanga, the School of Agronomy at the University of Antananarivo, and Direction des Eaux et Fôret, Madagascar, for granting me permission to conduct research at the Beza-Mahafaly Reserve, and for logistical help. I also thank Jonah Ratsimbazafy for his excellent research assistance. B.Z. Freed provided the data entry program.

LITERATURE CITED

Alexander BK (1970) Parental behaviour of adult male Japanese monkeys. Behaviour *36:*270–285.

Altmann J (1974) Observational study of behavior: Sampling methods. Behaviour *48:*1–41.

Altmann J (1980) Baboon Mothers and Infants. Cambridge, Mass.: Harvard University Press.

Breuggerman JA (1973) Parental care in a group of free-ranging rhesus monkeys. Folia Primatol. *20:*178–210.

Budnitz N and Dainis K (1975) *Lemur catta:* Ecology and behavior. In I Tattersall and RW Sussman (eds.): Lemur Biology. New York: Plenum, pp. 219–235.

Busse CD and Hamilton WJ III (1981) Infant carrying by male chacma baboons. Science *212:*1281–1283.

Deag JM and Crook JH (1971) Social behavior and "agonistic buffering" in the wild Barbary macaque, *Macaca sylvanus.* Folia Primatol. *15:*183–200.

Estrada A and Sandoval JM (1977) Social relations in a free-ranging troop of stumptail macaques (*Macaca arctoides*): Male care behavior. Primates *18:*793–813.

Fairbanks LA (1993) Juvenile vervet monkeys: Establishing relationships and practicing skills for the future. In ME Pereira and LA Fairbanks (eds.): Juvenile Primates: Life History, Development and Behavior. New York: Oxford University Press, pp. 211–227.

Gould L (1989) Infant social development and alloparenting in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. M.A. thesis, University of Alberta.

Gould L (1992) Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. Folia Primatol. *58:*72–83.

Gould L (1994) Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Ph.D. dissertation, Washington University.

Gould L (1996) Male-female affiliative relationships in naturally occurring ringtailed lemurs (*Lemur catta*) at Beza-Mahafaly Reserve, Madagascar. Am. J. Primatol. *39:*63–78.

Gould L (1997) Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at Beza-Mahafaly Reserve, Madagascar. Primates *38:*15–30.

Gould L, Sussman RW, and Sauther ML (1996) Demographic patterns from a long-term study of ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. XVIth Congress of the International Primatological Society and XIXth Conference of the American Society of Primatologists, University of Wisconsin-Madison (abstract).

Gouzoules H (1984) Social relations of males and infants in a troop of Japanese monkeys: A consideration of causal mechanisms. In DM Taub (ed.): Primate Paternalism. New York: Van Nostrand and Reinhold, pp. 127–145.

Hamilton WJ (1984) Significance of paternal investment by primates to the evolution of male-female associations. In DM Taub (ed.): Primate Paternalism. New York: Van Nostrand and Reinhold, pp. 127–145.

Hasegawa T and Hiraiwa M (1980) Social interactions of orphans observed in a free-ranging troop of Japanese monkeys. Folia Primatol. *33:*129–158.

Hill DA (1986) Social relationships between adult male and immature rhesus macaques. Primates *27:*425–440.

Hinde RA (1977) On assessing the basis of partner preferences. Behavior *62:*1–9.

Horrocks JA and Hunte A (1993) Interactions between juvenile and adult males in vervets: Implications for adult male turnover. In ME Pereira and LA Fairbanks (eds.): Juvenile Primates: Life History, Development and Behavior. New York: Oxford University Press, pp. 228–239.

Itani J (1959) Paternal care in the wild Japanese monkey, *Macaca fuscata.* Primates *2:*61–93.

Jolly A (1966) Lemur Behavior. Chicago: University of Chicago Press.

Jones KC (1983) Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. Folia Primatol. *40:*145–160.

Kummer H (1967) Tripartite relations in hamadryas baboons. In SA Altmann (ed.): Social Communication Among Primates. Chicago: University of Chicago Press.

Morland HS (1993) Seasonal behavioral variation and its relationships to thermoregulation in ruffed lemurs. In PM Kappeler and JU Ganzhorn (eds.): Lemur Social Systems and Their Ecological Basis. New York: Plenum, pp. 193–205.

Packer C (1980) Male care and exploitation of infants in *Papio anubis*. Anim. Behav. *28:*512–520.

Pereira ME, Kaufman R, Kappeler PM, and Overdorff DJ (1990) Female dominance does not characterize all of the Lemuridae. Folia Primatol. *55:*96–103.

Pereira ME and Weiss ML (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. Behav. Ecol. Sociobiol. *28:*141–152.

Ransom TW and Ransom BS (1971) Adult male-infant relations among baboons (*Papio anubis*). Folia Primatol. *16:*179–195.

Sauther ML (1991) Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Am. J. Phys. Anthropol. *84:*463–477.

Siegal S (1956) Nonparametric Statistics for the Behavioral Sciences. New York: McGraw-Hill.

Silk JB and Samuels A (1984) Triadic interactions among *Macaca radiata:* Passports and buffers. Am. J. Primatol. *6:*373–376.

Slater PJB (1978) Data collection. In PW Colgan (ed.): Ethology. New York: Wiley, pp. 7–24.

Smuts BB (1985) Sex and Friendship in Baboons. New York: Aldine.

Strum SC (1984) Why males use infants. In DM Taub (ed.): Primate Paternalism. New York: Van Nostrand and Reinhold, pp. 146–185.

Sussman RW (1977) Socialization, social structure and ecology of two sympatric species of *Lemur*. In S Chavalier-Skolnikoff and F Poirier (eds): Primate Bio-social Development. New York: Garland, pp. 515–529.

Sussman RW (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madgascar. Am. J. Phys. Anthropol. *84:*43–58.

Sussman RW (1992) Male life histories and inter-group mobility among ringtailed lemurs (*Lemur catta*). Int. J. Primatol. *13:*395–413.

Takahata Y (1982) Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop. Primates *23:*1–23.

Taub DM (1980) Testing the "agonistic buffering" hypothesis 1: The dynamics of participation in the triadic interaction. Behav. Ecol. Sociobiol. *6:*187–197.

Taub DM (1984) Male caretaking behavior among wild barbary macaques (*Macaca sylvanus*). In DM Taub (ed.): Primate Paternalism. New York: Van Nostrand and Reinhold, pp. 20–55.

Taylor LL (1986) Kinship, dominance, and social organization in a semi-free-ranging group of ring-tailed Lemurs (*Lemur catta*). Ph.D. dissertation, Washington University.

Taylor LL and Sussman RW (1987) A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. Int. J. Primatol. *6:*601–614.

Vessey SH and Meikle DB (1984) Free living rhesus monkeys: Adult male interactions with infants and juveniles. In DM Taub (ed.) Primate Paternalism. New York: Van Nostrand and Reinhold, pp. 113–126.